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TWO REVOLUTIONS: COPERNICUS AND DARWIN

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Election to the distinguished Serbian Academy of Sciences and Arts is a very great honor. My election as a Foreign Member is, indeed, a great distinction that I shall henceforward treasure with both pride and humility. With pride, because of the eminent distinction of the Academy. With humility, because how could I possibly have deserved such recognition? I accept this honor not as an earned merit but as an undeserved and much valued gift.

This gift is particularly precious to me because of my love for the beautiful land of Serbia and its historical and cultural treasures, which I have appreciated and enjoyed on numerous visits that started more than a quarter of a century ago. Beyond the land and its riches, there is my scientific association and long-standing friendship with Serbian scientists.

Summary of the Argument

I will propose that Darwin's most significant intellectual contribution is that he brought the origin and diversity of organisms into the realm of science. The Copernican Revolution consisted in a commitment to the postulate that the universe is governed by natural laws that account for natural phenomena. Darwin completed the Copernican Revolution by extending that commitment to the living world.

I will explain that natural selection is a creative process that can account for the appearance of genuine novelty. How natural selection creates is shown with a simple example and clarified with two analogies, artistic creation and the "typing monkeys," with which it shares important similarities and differences. The creative power of natural selection arises from a distinctive interaction between chance and necessity, or between random and deterministic processes.

Copernicus and Darwin

There is a priggish version of the history of the ideas that sees a parallel between Copernicus' and Darwin's monumental intellectual contributions, which are said to have eventuated two revolutions. According to this version, the Copernican Revolution consisted in displacing the Earth from its previously accepted locus as the center of the universe, moving it to a subordinate place as one more planet revolving around the sun. In congruous manner, this version affirms, the Darwinian Revolution consisted in displacing humans from their position as

the center of life on Earth, with all other species created for the purpose of humankind, and placing humans instead as one species among many in the living world, so that humans are related to chimpanzees, gorillas, and other species by shared common ancestry. Copernicus had accomplished his revolution with the heliocentric theory of the solar system. Darwin's achievement emerged from his theory of organic evolution.

I will proffer that this version of the two revolutions is inadequate: what it says is true, but it misses what is most important about these two intellectual revolutions, namely that they ushered in the beginning of science in the modern sense of the word. These two revolutions may jointly be seen as the one Scientific Revolution, with two stages, the Copernican and the Darwinian.

Darwin is deservedly given credit for the theory of biological evolution, because he accumulated evidence demonstrating that organisms evolve and discovered the process, natural selection, by which they evolve their functional organization. But the import of Darwin's *The Origin of Species,* published in 1859, is that it completed the Copernican Revolution, initiated three centuries earlier, and thereby radically changed our conception of the universe and the place of mankind in it.

The Copernican Revolution was launched with the publication in 1543, the year of Nicolaus Copernicus' death, of his *De revolutionibus orbium celestium* (On the Revolutions of the Celestial Spheres), and bloomed with the publication in 1687 of Isaac Newton's *Philosophiae naturalis principia mathematica* (The Mathematical Principles of Natural Philosophy).

The discoveries of Copernicus, Kepler, Galileo, Newton, and others, in the sixteenth and seventeenth centuries, had gradually ushered in a conception of the universe as matter in motion governed by natural laws. It was shown that the earth is not the center of the universe, but a small planet rotating around an average star; that the universe is immense in space and in time; and that the motions of the planets around the sun can be explained by the same simple laws that account for the motion of physical objects on our planet. (Laws such as $f = m$ x a, *force* = *mass* x *acceleration*, or the inverse-square law of attraction, $f = g(m_1m_2)/r^2$.) These and other discoveries greatly expanded human knowledge, but the conceptual revolution they brought about was more fundamental yet: a commitment to the postulate that the universe obeys immanent laws that account for natural phenomena. The workings of the universe were brought into the realm of science: explanation through natural laws. Physical phenomena could be accounted for whenever the causes were adequately known.

Darwin completed the Copernican Revolution by drawing out for biology the ultimate conclusion of the notion of nature as a lawful system of matter in motion. The adaptations and diversity of organisms, the origin of novel and highly organized forms, the origin of mankind itself, could now be explained by an orderly process of change governed by natural laws.

The origin of organisms and their marvelous adaptations were attributed, before Darwin, to the design of an omniscient Creator. God had created the birds and bees, the fish and corals, the trees in the forest, and best of all, man. God had given man eyes so that he might see, and He had provided fish with gills to breathe in water. William Paley, in his *Natural Theology* of 1802, had argued that the functional design of organisms manifests the existence of an all-wise Creator. Wherever there is design, there is a designer; the existence of a watch evinces the existence of a watchmaker. This "argument-from-design" to demonstrate the existence of God was further

elaborated by the eight *Bridgewater Treatises,* published in England between 1833 and 1840, to set forth "the Power, Wisdom, and Goodness of God as manifested in the creation." Other philosophers and theologians had advanced similar arguments in various parts of the world.

The advances of physical science had, thus, driven mankind's conception of the universe to a split-personality state of affairs, which persisted well into the mid-nineteenth century. Scientific explanations, derived from natural laws, dominated the world of nonliving matter, on the earth as well as in the heavens. Supernatural explanations, depending on the unfathomable deeds of the Creator, accounted for the origin and configuration of living creatures—the most diversified, complex, and interesting realities of the world.

It was Darwin's genius to resolve this conceptual schizophrenia. Darwin completed the Copernican Revolution by drawing out for biology the notion of nature as a lawful system of matter in motion that human reason can explain without recourse to extra-natural agencies.

Darwin's Greatest Discovery

The conundrum faced by Darwin can hardly be overestimated. The strength of the argument-from-design to demonstrate the role of the Creator is easily set forth. Wherever there is function or design, we look for its author. Paley had belabored this argument with great skill and profusion of detail. It was Darwin's greatest accomplishment to show that the complex organization and functionality of living beings can be explained as the result of a natural process, natural selection, without any need to resort to a Creator or other external agent. The origin and adaptation of organisms in their profusion and wondrous variations were thus brought into the realm of science.

Darwin accepted that organisms are "designed" for certain purposes, i.e., they are functionally organized. Organisms are adapted to certain ways of life and their parts are adapted to perform certain functions. Fish are adapted to live in water, kidneys are designed to regulate the composition of blood, the human hand is made for grasping. But Darwin went on to provide a natural explanation of the design. The seemingly purposeful aspects of living beings could now be explained, like the phenomena of the inanimate world, by the methods of science, as the result of natural laws manifested in natural processes.

The central argument of the theory of natural selection is summarized by Darwin in *The Origin of Species* as follows: "As more individuals are produced than can possibly survive, there must in every case be a struggle for existence, either one individual with another of the same species, or with the individuals of distinct species, or with the physical conditions of life... Can it, then, be thought improbable, seeing that variations useful to man have undoubtedly occurred, that other variations useful in some way to each being in the great and complex battle of life, should sometimes occur in the course of thousands of generations? If such do occur, can we doubt (remembering that more individuals are born than can possibly survive) that individuals having any advantage, however slight, over others, would have the best chance of surviving and of procreating their kind? On the other hand, we may feel sure that any variation in the least degree injurious would be rigidly destroyed. This preservation of favorable variations and the rejection of injurious variations, I call Natural Selection."

Darwin's argument addresses the same issues as Paley's: how to account for the adaptive configuration of organisms, the obvious "design" of their parts to fulfill certain functions. Darwin

argues that hereditary adaptive variations ("variations useful in some way to each being") occasionally appear, and that these are likely to increase the reproductive chances of their carriers. The success of pigeon fanciers and animal breeders clearly evinces the occasional occurrence of useful hereditary variations.

Over the generations favorable variations will be preserved, multiplied and conjoined; injurious ones will be eliminated. In one place, Darwin adds: "I can see no limit to this power [natural selection] in slowly and beautifully *adapting* each form to the most complex relations of life." Natural selection was proposed by Darwin primarily to account for the adaptive organization, or "design," of living beings; it is a process that preserves and promotes adaptation. Evolutionary change through time and evolutionary diversification (multiplication of species) are not directly promoted by natural selection (hence, the so-called "evolutionary stasis" emphasized by the theory of punctuated equilibrium), but they often ensue as by-products of natural selection fostering adaptation.

There is a possible reading of Darwin's *Origin of Species* that sees it, first and foremost, as a sustained effort to solve Paley's problem within a scientific explanatory framework. It is, indeed, how I interpret Darwin's masterpiece. The Introduction and Chapters I through VIII explain how natural selection accounts for the adaptations and behaviors of organisms, their "design." The extended argument starts in chapter I, where Darwin describes the successful selection of domestic plants and animals and, with considerable detail, the success of pigeon fanciers seeking exotic "sports." This evidence manifests what selection can accomplish using spontaneous variations beneficial to man.

The ensuing chapters extend the argument to variations propagated by natural selection (i.e., reproductive success) for the benefit of the organisms, rather than by artificial selection for traits desirable to humans. Organisms exhibit design, but it is not "intelligent design," imposed by God as a Supreme Engineer, but the result of natural selection promoting the adaptation of organisms to their environments. Organisms exhibit complexity, but it is not "irreducible complexity" emerged all of a sudden in its current elaboration, but has arisen gradually and cumulatively, step by step, promoted by the adaptive success of individuals with incrementally more complex elaborations.

If Darwin's explanation of the adaptive organization of living beings is correct, evolution necessarily follows as organisms become adapted to different environments and to the changing conditions of all environments, and as hereditary variations become available that improve, at a particular time and in a particular place, the organisms' chances of survival and reproduction. The *Origin*'s evidence for biological evolution is central to Darwin's explanation of "design," because his explanation postulates the occurrence of biological evolution, which he therefore seeks to demonstrate in most of the remainder of the book (chapters IX – XIII), returning to the original theme in the concluding chapter XIV.

In the last paragraph of the *Origin*, Darwin eloquently returns, indeed, to the dominant theme of adaptation or design: "It is interesting to contemplate an entangled bank, clothed with many plants of many kinds, with birds singing on the bushes, with various insects flitting about, and with worms crawling through the damp earth, and to reflect that these *elaborately constructed* forms, *so different* from each other, and dependent on each other *in so complex a manner*, have all been produced by laws acting around us. […] Thus, from the war of nature,

from famine and death, the most exalted object which we are capable of conceiving, namely, the production of the higher animals, directly follows. There is grandeur in this view of life, with its several powers, having been originally breathed into a few forms or into one; and that, whilst this planet has gone cycling on according to the fixed law of gravity, from so simple a beginning *endless forms most beautiful and most wonderful* have been, and are being, evolved" [my emphasis].

Natural Selection and the "Design" of Organisms

The modern understanding of the principle of natural selection is formulated in genetic and statistical terms as differential reproduction. Natural selection implies that some genes and genetic combinations are transmitted to the following generations with a higher probability than their alternates. Such genetic units will become more common in subsequent generations and their alternates less common. Natural selection is a statistical bias in the relative rate of reproduction of alternative genetic units.

Natural selection does not operate as a sieve that retains the rarely arising useful genes and lets go the more frequently arising harmful mutants; at least, not only. Natural selection acts in the filtering way of a sieve, but it is much more than a purely negative process, for it is able to generate novelty by increasing the probability of otherwise extremely improbable genetic combinations. Natural selection is thus a creative process. It does not "create" the entities upon which it operates, but it produces adaptive (functional) genetic combinations that could not have existed otherwise.

The creative role of natural selection must not be understood in the sense of the "absolute" creation that traditional Christian theology predicates of the Divine act by which the universe was brought into being *ex nihilo*, or in the manner of creation in which Paley assumes that God, the Supreme Engineer, had created the adaptations of organisms. Natural selection may rather be compared to a painter who creates a picture by mixing and distributing pigments in various ways over the canvas. The canvas and the pigments are not created by the artist but the painting is. It is inconceivable that a random combination of the pigments might result in the orderly whole that is the final work of art, say Leonardo da Vinci's *Mona Lisa*. In the same way, the combination of genetic units which carries the hereditary information responsible for the formation of the vertebrate eye could have never been produced by a random process like mutation. Not even if we allow for the three billion years plus during which life has existed on earth. The complicated anatomy of the eye, like the exact functioning of the kidney, are the result of a nonrandom process—natural selection.

How natural selection, a purely material process, can generate novelty in the form of accumulated hereditary information may be illustrated by the following example. Some strains of the colon bacterium, *Escherichia coli*, in order to be able to reproduce in a culture medium, require that a certain substance, the amino acid histidine, be provided in the medium. When a few such bacteria are added to ten cubic centimeters of liquid culture medium, they multiply rapidly and produce between twenty and thirty billion bacteria in a few hours. Spontaneous mutations to streptomycin resistance occur in normal (i.e., sensitive) bacteria at rates of the order of one in one hundred million ($1x10^{-8}$) cells. In the bacterial culture we expect between two hundred and three hundred bacteria to be resistant to streptomycin due to spontaneous mutation. If a proper concentration of the antibiotic is added to the culture, only the resistant cells survive. The two or

three hundred surviving bacteria will start reproducing, however, and allowing one or two days for the necessary number of cell divisions, twenty or so billion bacteria are produced, all resistant to streptomycin. Among cells requiring histidine as a growth factor, spontaneous mutants able to reproduce in the absence of histidine arise at rates of about four in one hundred million ($4x10^{-8}$) bacteria. The streptomycin resistant cells may now be transferred to a culture with streptomycin but with no histidine. Most of them will not be able to reproduce, but about one thousand will and will start reproducing until the available medium is saturated.

Natural selection has produced in two steps bacterial cells resistant to streptomycin and not requiring histidine for growth. The probability of the two mutational events happening in the same bacterium is of about four in ten million billion ($1x10^{-8}x4x10^{-8} = 4x10^{-16}$) cells. An event of such low probability is unlikely to occur even in a large laboratory culture of bacterial cells. With natural selection, cells having both properties are the common result.

Critics have sometimes alleged as evidence against Darwin's theory of evolution examples showing that random processes cannot yield meaningful, organized outcomes. It is thus pointed out that a series of monkeys randomly striking letters on a typewriter would never write *The Origin of Species*, even if we allow for millions of years and many generations of monkeys pounding at typewriters.

This criticism would be valid if evolution would depend only on random processes. But natural selection is a non-random process that promotes adaptation by selecting combinations that "make sense," i.e., that are useful to the organisms. The analogy of the monkeys would be more appropriate if a process existed by which, first, meaningful words would be chosen every time they appeared on the typewriter; and then we would also have typewriters with previously selected words rather than just letters in the keys, and again there would be a process to select meaningful sentences every time they appeared in this second typewriter. If every time words such as "the," "origin," "species," and so on, appeared in the first kind of typewriter, they each became a key in the second kind of typewriter, meaningful sentences would occasionally be produced in this second typewriter. If such sentences became incorporated into keys of a third type of typewriter, in which meaningful paragraphs were selected whenever they appeared, it is clear that pages and even chapters "making sense" would eventually be produced. The end product would be an “irreducibly complex” text.

We need not carry the analogy too far, since the analogy is not fully satisfactory, but the point is clear. Evolution is not the outcome of purely random processes, but rather there is a "selecting" process, which picks up adaptive combinations because these reproduce more effectively and thus become established in populations. These adaptive combinations constitute, in turn, new levels of organization upon which the mutation (random) plus selection (non-random or directional) process again operates. The complexity of organization of animals and plants is “irreducible” to simpler components in one or very few steps, but not thorough the millions and millions of generations, and the multiplicity of steps and levels made possible by eons of time.

Natural Selection as a Stepwise Process

The critical point is that evolution by natural selection is an incremental process, operating over eons of time and yielding organisms better able to survive and reproduce than others, which typically differ from one another at any one time only in small ways; for example,

the difference between having or lacking an enzyme able to catalyze the synthesis of the amino acid histidine.

Notice also that increased complexity is not a necessary outcome of natural selection, although such increases occur from time to time, so that, although rare, they are very conspicuous over time's eons. Increased complexity is not a necessary consequence of evolution by natural selection, but rather emerges occasionally as a matter of statistical bias. The longest living organisms on Earth are microscopic bacteria, which have continuously existed on our planet for three and a half billion years and yet exhibit no greater complexity than their old time ancestors. More complex organisms came about much later, without the elimination of their simpler relatives. For example, the primates appeared on earth some fifty million years ago and our species, *Homo sapiens*, came about two hundred thousand years ago.

As illustrated by the bacterial example, natural selection produces combinations of genes that would otherwise be highly improbable because natural selection proceeds stepwise. The vertebrate eye did not appear suddenly in all its present perfection. Its formation required the appropriate integration of many genetic units, and thus the eye could not have resulted from random processes alone, nor did it come about suddenly or in a few steps. The ancestors of today's vertebrates had for more than half a billion years some kind of organs sensitive to light. Perception of light, and later vision, were important for these organisms' survival and reproductive success. Accordingly, natural selection favored genes and gene combinations increasing the functional efficiency of the eye. Such genetic units gradually accumulated, eventually leading to the highly complex and efficient vertebrate eye. Natural selection can account for the rise and spread of genetic constitutions, and therefore of types of organisms, that would never have existed under the uncontrolled action of random mutation. In this sense, natural selection is a creative process, although it does not create the raw materials—the genes—upon which it acts.

Chance and Necessity

There is an important respect in which an artist makes a poor analogy of natural selection. A painter has a preconception of what he wants to paint and will consciously modify the painting so that it represents what he wants. Natural selection has no foresight, nor does it operate according to some preconceived plan. Rather it is a purely natural process resulting from the interacting properties of physicochemical and biological entities.

Natural selection is simply a consequence of the differential multiplication of living beings, as pointed out. It has some appearance of purposefulness because it is conditioned by the environment: which organisms reproduce more effectively depends on what variations they possess that are useful in the place and at the time where the organisms live. But natural selection does not anticipate the environments of the future; drastic environmental changes may be insuperable to organisms that were previously thriving. Species extinction is the common outcome of the evolutionary process. The species existing today represent the balance between the origin of new species and their eventual extinction. More than 99 percent of all species that ever lived on Earth have become extinct without issue. These may have been more than one billion species; the available inventory of living species has identified and described less than two million out of some ten million estimated to be now in existence.

The team of typing monkeys is also a bad analogy of evolution by natural selection, because it assumes that there is "somebody" who selects letter combinations and word combinations that make sense. In evolution there is no one selecting adaptive combinations. These select themselves because they multiply more effectively than less adaptive ones.

There is a sense in which the analogy of the typing monkeys is better than the analogy of the artist, at least if we assume that no particular statement was to be obtained from the monkeys' typing endeavors, but just any statements making sense. Natural selection does not strive to produce predetermined kinds of organisms, but only organisms that are adapted to their present environments. Which characteristics will be selected depends on which variations happen to be present at a given time in a given place. This in turn depends on the random process of mutation, as well as on the previous history of the organisms (i.e., on the genetic make-up they have as a consequence of their previous evolution). Natural selection is an "opportunistic" process. The variables determining in what direction it will go are the environment, the preexisting constitution of the organisms, and the randomly arising mutations.

Thus, adaptation to a given environment may occur in a variety of different ways. An example may be taken from the adaptations of plant life to the desert climate. The fundamental adaptation is to the condition of dryness, which involves the danger of desiccation. During a major part of the year, sometimes for several years in succession, there is no rain. Plants have accomplished the urgent necessity of saving water in different ways. Cacti have transformed their leaves into spines, having made their stems into barrels storing a reserve of water; photosynthesis is performed on the surface of the stem instead of in the leaves. Other plants have no leaves during the dry season, but after it rains they burst into leaves and flowers and produce seeds. Ephemeral plants germinate from seeds, grow, flower, and produce seeds—all within the space of the few weeks while rainwater is available; the rest of the year the seeds lie quiescent in the soil.

The opportunistic character of natural selection is also well evidenced by the phenomenon of adaptive radiation. The evolution of drosophila flies in Hawaii is a relatively recent adaptive radiation. There are about 1,500 drosophila species in the world. Approximately 500 of them have evolved in the Hawaiian archipelago, which has a small land area, about thirty percent of the size of Serbia. Moreover, the morphological, ecological, and behavioral diversity of Hawaiian drosophila exceeds that of drosophila in the rest of the world. There are more than one thousand species of land snails in Hawaii, all of which have evolved in the archipelago. There are 72 bird species, all of which but one exist nowhere else.

Why should have such "explosive" evolution have occurred in Hawaii? The overabundance of drosophila flies there contrasts with the absence of many other insects. The ancestors of Hawaiian drosophila reached the archipelago before other groups of insects did, and thus they found a multitude of unexploited opportunities for living. They responded by a rapid adaptive radiation; although they are all derived from a single colonizing species, they adapted to the diversity of opportunities available in diverse places or at different times by developing appropriate adaptations, which range broadly from one to another species. The geographic remoteness of the Hawaiian archipelago seems, in any case, a more reasonable explanation for these explosions of diversity of a few kinds of organisms than assuming an inordinate preference on the part of the Creator for providing the archipelago with numerous drosophila, but not with other insects, or a peculiar distaste for creating land mammals in Hawaii, since none existed there until introduced by humans.

The process of natural selection can explain the adaptive organization of organisms, as well as their diversity and evolution, as a consequence of their adaptation to the multifarious and ever changing conditions of life. The fossil record shows that life has evolved in a haphazard fashion. The radiations, expansions, relays of one form by another, occasional but irregular trends, and the ever-present extinctions, are best explained by natural selection of organisms subject to the vagaries of genetic mutation and environmental challenge.

The scientific account of these events does not necessitate recourse to a preordained plan, whether imprinted from without by an omniscient and all-powerful designer, or resulting from some immanent force driving the process towards definite outcomes. Biological evolution differs from a painting or an artifact in that it is not the outcome of preconceived design.

Natural Selection and Design

Natural selection accounts for the "design" of organisms, because adaptive variations tend to increase the probability of survival and reproduction of their carriers at the expense of maladaptive, or less adaptive, variations. Neither William Paley nor any other author before Darwin, was able to discern that there is a natural process (namely, natural selection) that is not random, but rather is oriented and able to generate order or "create." The traits that organisms acquire in their evolutionary histories are not fortuitous but determined by their functional utility to the organisms, "designed" as it were to serve their life needs.

Chance is, nevertheless, an integral part of the evolutionary process. The mutations that yield the hereditary variations available to natural selection arise at random, independently of whether they are beneficial or harmful to their carriers. But this random process (as well as others that come to play in the great theatre of life) is counteracted by natural selection, which preserves what is useful and eliminates the harmful. Without heredity mutation, evolution could not happen because there would be no variations that could be differentially conveyed from one to another generation. But without natural selection, the mutation process would yield disorganization and extinction because most mutations are disadvantageous. Mutation and selection have jointly driven the marvelous process that starting from microscopic organisms has yielded orchids, birds, and humans.

The theory of evolution conveys chance and necessity jointly intricated in the stuff of life; randomness and determinism interlocked in a natural process that has spurted the most complex, diverse, and beautiful entities in the universe: the organisms that populate the earth, including humans who think and love, endowed with free will and creative powers, and able to analyze the process of evolution itself that brought them into existence. This is Darwin's fundamental discovery, that there is a process that is creative though not conscious. And this is the conceptual revolution that Darwin completed: that everything in nature, including the "design" of living organisms, can be accounted for as the result of natural processes governed by natural laws. This is nothing if not a fundamental vision that has forever changed how mankind perceives itself and its place in the universe.

Appendix.

I want particularly to recognize my treasured four decades-long, intimate friendship with Academician Dragoslav Marinković. It is many years ago that we began our collaboration

on population and evolutionary genetics research projects. Our first joint publications appeared in 1975 in *Genetics*, a United States journal, and in *Genetical Research*, a British journal. I list as an appendix ca. ten joint scientific publications, which I consider of notable significance.

THE JOINT PUBLICATIONS OF SERBIAN GENETICISTS AND FRANCISCO J. AYALA:

CLUSTER, P.D., D., MARINKOVIĆ, R.W., ALLARD, F.J. AYALA (1987): Correlations between development rates, enzyme activities, ribosomal DNA spacer-length phenotypes, and adaptation in *Drosophila melanogaster*. Proc. Natl. Acad. Sci. USA, *84*:10-614.

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MARINKOVIĆ, D. and F.J. AYALA (1975): Fitness of allozyme variants in Drosophila pseudoobscura. II. Selection at the *Est-5*, *Odh*, and *Mdh-2* loci. Genetical Research, *24*:137-149.

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MARINKOVIĆ, D. and F.J. AYALA (1986): Genetic variation for rate of development in natural populations of *Drosophila melanogaster*. Genetica, *71*:123-132.

MARINKOVIĆ, D. and F.J. AYALA (1986): Selection for different rates of embryonic develop- ment in *Drosophila melanogaster* and *Drosophila simulans*. Genetika, *18*:205-219.

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TUCIĆ, N., F.J., AYALA, D., MARINKOVIĆ (1981): Correlation between recombination frequency and fitness in *Drosophila melanogaster*. Genetica, *56*:61-69.